

Intrinsic Competition and Competitor-Free-Space Influence the Coexistence of Parasitoids (Hymenoptera: Braconidae: Opiinae) of Neotropical Tephritidae (Diptera)

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ABSTRACT Endoparasitoid larvae may eliminate heterospecific competitors by physical or physiological means. The outcomes of these intrinsic competitions are often predictable with one species typically eliminating the other. The opiine braconids *Doryctobracon areolatus* (Szepligeti) and *Utetes anastrephae* (Viereck) are among the most common native parasitoids of frugivorous Tephritidae in the Neotropics and subtropics. *U. anastrephae* is typically the victor in intrinsic interactions with *D. areolatus*, but the later has a longer ovipositor and may find a competitor-free-space in larger fruit whose hosts are beyond the reach of *U. anastrephae*. An Asian opiine species, *Diachasmimorpha longicaudata* (Ashmead) has been introduced throughout much of the Americas. Its ovipositor is longer than that of *D. areolatus* and if it is a superior intrinsic competitor it should be able to cause local extinctions of *D. areolatus*. The outcomes of sequential ovipositions by *D. longicaudata* and *D. areolatus* and *U. anastrephae* found that *D. longicaudata* significantly suppresses development of *D. areolatus*. However, competitions between *D. longicaudata* and *U. anastrephae* were more equal. The denial of competitor free space may account for the gradual replacement of *D. areolatus* by *D. longicaudata* in Florida where both species were introduced ≈40 yr ago. *Diachasmimorpha longicaudata* and *D. areolatus* continue to coexist in Mexico and this could be because of greater abiotic and biotic environmental complexity that allows for separate niches. Establishment or augmentative releases of *D. longicaudata* could result in elimination of native parasitoids and this should be considered before its introduction.

KEY WORDS ovipositor length, host-fruit size, *Diachasmimorpha*, *Doryctobracon*, *Utetes*

An insect species is often exploited by multiple parasitoids thereby creating the possibility of interspecific competition (Hawkins 1994, 2000). Even where there is little negative interaction among the members of a presently existing guild of natural enemies, the temporal and spatial niche separations that prevent direct encounters may be evidence of previous competition and selection for its avoidance (e.g., Tschamtko 1992; the “ghost of competition past,” Connell 1980). However, there are situations where interspecific interactions could regularly occur and female parasitoids have an initial opportunity to avoid placing their offspring in competitive situations (Boivin and Brodeur 2006). They may discriminate against already parasitized hosts by rejecting hosts marked with an Oviposition Detering Pheromone (ODP) or a cue representing a previous parasitoid-visit such as feces

(Rousse et al. 2007). Conspecific, even individual, ODP recognition is common, and although rarer, recognition of heterospecific ODPs (or their equivalent) does occur. There are at least two examples within the opiine braconid parasitoids of Tephritidae: *Diachasmimorpha tryoni* Cameron is less likely to oviposit in larvae that have already been attacked by *Fopius arisanus* (Sonan) (Wang and Messing 2003) and *Utetes anastrephae* (Viereck) discriminates against hosts parasitized by *Doryctobracon areolatus* (Szepligeti), although the opposite is not the case (Aluja et al. 2013). Occasionally, adult female parasitoids will aggressively defend a host they have parasitized (Griffiths and Godfray 1988), add substances that make the host physiologically unsuited for other eggs or larvae (Silvers and Nappi 1986) or even kill already existing competitors with venom (Wang and Messing 2004).

When adult female foraging or oviposition decisions or aggressive interventions fail to keep their offspring from confronting an immature heterospecific, the final competition, for endoparasitoids at least, takes place within the host itself and between the heterospecific larvae themselves. Larvae may starve, suffocate, or poison other females' progeny by inducing physiolog-

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ical changes in the host (Fisher 1961), or attack potential competitors with enlarged mandibles or armored caudal appendages typical of many motile first instar larvae (Salt 1961).

The outcomes of such intrinsic competitions are often predictable, that is, one species is more likely to develop than another given certain conditions that can include the relative times of oviposition and host size and condition (Godfray 1994, Mills 2003, Wang et al. 2003). *U. anastrephae* is typically victorious over *D. areolatus* if the two ovipositions occur within 24 h of each other, and there is circumstantial evidence that the greater size and larger mandibles of first instar *U. anastrephae* play a role in these victories (Aluja et al. 2013). Given the wide-spread sympatry of these two Neotropical species and the similarities in their *Anastrepha* spp. hosts (Ovruski et al. 2000), how does the inferior competitor (*D. areolatus*) coexist with its superior (*U. anastrephae*)? One possibility is that the longer ovipositor of *D. areolatus* allows it to exploit tephritid larvae in larger fruit that are out-of-reach and unavailable to *U. anastrephae* (Sivinski et al. 1997, 1998, 2001). Thus, it has been hypothesized that the relatively long ovipositor of *D. areolatus* creates a "competitor-free-space" in which it can thrive despite *U. anastrephae* (Aluja et al. 2013).

A role for competitor avoidance in the structuring of a parasitoid guild depends upon significant competition for limited hosts and this can seasonally be the case among fruit fly parasitoids. For example, tephritid parasitism in Mexican fruits such as *Spondias mombin* L. sometimes exceeds 80% (López et al. 1999) and Florida parasitoids can inflict parasitism rates of >90% on the fly larvae in *Eugenia uniflora* L. (Sivinski et al. 1996). Because principal host fruits are often sequentially available, there will be times when tephritid populations are concentrated in fruits that offer little shelter and here they may undergo periods of intense exposure to parasitoids and their parasitoids to periods of intense intra- and interspecific competition.

A prediction of the "competition-avoidance-through-a-longer-ovipositor" hypothesis is that the introduction of a superior intrinsic competitor with an even longer ovipositor would result in the local extinction of *D. areolatus*. This experiment may have been inadvertently performed when first *D. areolatus* and then the Asian *Diachasmimorpha longicaudata* (Ashmead) were introduced into Florida to biologically control *Anastrepha suspensa* (Loew), the Caribbean fruit fly (Baranowski et al. 1993). At first, *D. areolatus* was well established in Florida. However, after the introduction of *D. longicaudata* it disappeared from the southern portion of the peninsula and eventually was found only in the northern part of *A. suspensa* range (Eitam et al. 2004). It appeared that *D. areolatus* had been widely displaced by a superior competitor and was only able to persist on the margins of its host's range perhaps because of an ability to better survive cooler weather and cold's seasonal consequences in terms of host availability.

D. longicaudata is a formidable intrinsic competitor and able to eliminate both *Fopius persulcatus* (Silves-

tri) and *F. arisanus* when physical competitions take place between first-instar larvae (Palacio et al. 1991, Wang et al. 2008). The first-instar larvae of *D. longicaudata* also physically kill those of its congener *D. tryoni* (Ramadan et al. 1994). If *D. longicaudata* is a superior intrinsic competitor to *D. areolatus* as well, then a means by which it could out-compete *D. areolatus* is established. As the specific name "*longicaudata*" (long tail) justly describes, *D. longicaudata* also has a long ovipositor, substantially longer than that of *D. areolatus* (Sivinski et al. 2001). Thus, a superiorly competitive *D. longicaudata* would also eliminate the competitor-free-space available to *D. areolatus* in larger host fruit when interacting with just *U. anastrephae*.

In the current study we determined the outcome of intrinsic competition between *D. areolatus* and *D. longicaudata*, and then examined intrinsic competition between *D. longicaudata* and *U. anastrephae*, a parasitoid that also occurs in Florida. After this, we considered if the outcomes of intrinsic competitions are consistent with the distributions of the various parasitoid species in both Florida and Mexico. Finally, we discuss the relevance of these findings to fruit fly biological control tactics.

Materials and Methods

Experimental Insects. *A. suspensa* larvae were obtained from a mass-reared colony maintained by the Florida Department of Agriculture and Consumer Services, Division of Plant Industry (DPI), Gainesville, FL (FDACS DPI 1995). The colony had been initiated from wild stock several years previously. *D. longicaudata* were reared at the U.S. Department of Agriculture-Agriculture Research Services (USDA-ARS), Center for Medical, Agricultural and Veterinary Entomology (CMAVE), Gainesville, FL. The colony was 10 yr old, but 100-1000 wild individuals had been integrated into it semiannually. *D. areolatus* were originally obtained from colonies at the Instituto de Ecología (IdE), Xalapa, Veracruz, Mexico (Aluja et al. 2009) and then reared at CMAVE. *U. anastrephae* were obtained from a 3-10 generations-old colony maintained at CMAVE and initiated with insects collected throughout southern Florida. Voucher specimens are available at CMAVE and IdE.

Experimental Conditions. Female parasitoids, 7-10 d of age, presumably mated and with previous oviposition opportunities, were placed in 20 by 20 by 20 cm cages, screened on three sides. Temperature was 23°C, relative humidity (RH) ≈60% and lighting was provided by overhead fluorescent bulbs.

Treatment Regimens. Females were provided hosts in an Oviposition Device (OD) that consisted of a 3 cm d and 0.5 cm h embroidery ring supporting a sandwich of organdy cloth (ventral side) and parafilm (dorsal side; American National Can, Menasha, WI). Inside this sandwich were 20 *A. suspensa* larvae (third instar; 6-7 d of age), a small amount of artificial diet (FDACS 1995) and a thin slice of "Bartlett" pear (*Pyrus communis* L.). The parafilm had been previously wrapped

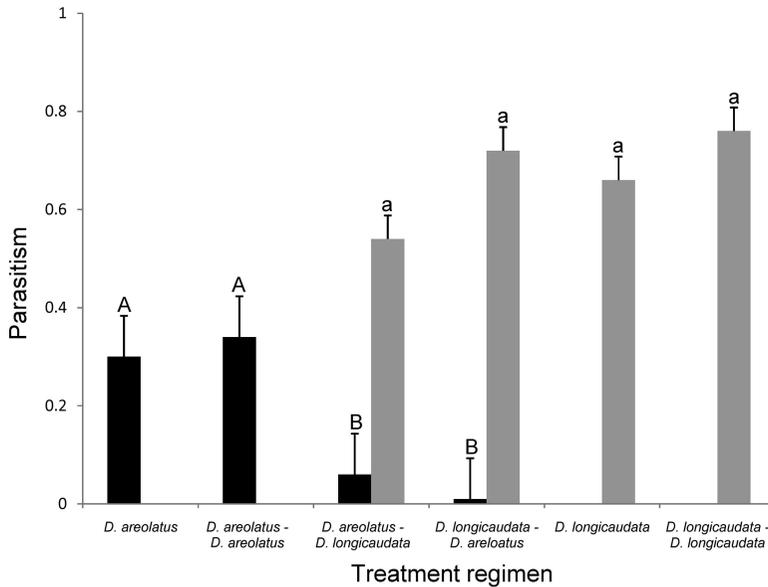


Fig. 1. The mean proportions (SE) of the adult insects that emerged from cohorts of *Anastrepha suspensa* larvae that were the parasitoids *Doryctobracon areolatus* (*D. areolatus*) or *Diachasmimorpha longicaudata* (*D. longicaudata*) ($n_{\text{parasitoidx}}/\Sigma$ adult insects). Host cohorts were exposed to either a single female of a particular species, two females of a species sequentially, or a female of first one species and then another and vice versa. Means sharing a letter were not significantly different (capital letters refer to comparisons of mean *D. areolatus* parasitism and lower-case letters to those of *D. longicaudata*).

around a pear for 24 h to adsorb possible oviposition cues (Eitam et al. 2003). All ODs were prepared in the morning of the experiments and kept in the same environment until daily experiments were completed.

To observe the effects of exposure to a potential intrinsic competitor, the parasitism inflicted by cohorts of either *D. areolatus* (*Da*) or *U. anastrephae* (*Ua*) were compared with their parasitism rates when their hosts were immediately exposed to *D. longicaudata* (*Dl*). To make these comparisons, there were six different types of exposure of hosts to each pair of parasitoid species (*Dl* vs. either *Da* or *Ua*) and an additional control where hosts were placed under experimental conditions but not exposed to parasitoids. These regimens were: 1) hosts exposed to either *Da* or *Ua* for 3 h (parasitism in the absence of a potential intrinsic competitor); 2) hosts exposed to either *Da* or *Ua* for 3 h and then to a different cohort of conspecifics for 3 h (allowed comparisons of pupal-mortalities and cumulative parasitisms with the longer sequential exposures to different species); 3) hosts exposed to either *Da* or *Ua* for 3 h followed by exposure to *Dl* for 1 h (parasitism in the presence of a potential intrinsic competitor; *Dl*-exposure time was shorter because it oviposites more readily in captivity than the other species); 4) hosts exposed to *Dl* for 1 h followed by exposure of either *Da* or *Ua* for 3 h (as above but with exposures reversed to control for order effects); 5) hosts exposed to *Dl* for 1 h (parasitism in the absence of a potential intrinsic competitor); 6) hosts exposed to *Dl* for 1 h and then to a different cohort of conspecifics for 1 h (allowed comparisons of pupal-mortalities and cumulative parasitism with sequential exposures to different species).

After completion of exposure to parasitoids, cohorts of host larvae were transferred to 50 ml plastic cups containing a pupation medium, moist vermiculite, and covered with cloth to allow ventilation. Cups were held in an incubator ($25 \pm 2^\circ\text{C}$ and $70 \pm 10\%$ of RH) for 20 d, at which time all eclosed adults and intact pupae were counted and identified. There were 20 replicates of each regimen of each parasitoid species comparison.

Parasitism ($n_{\text{parasitoidx}}/\Sigma$ adult insects) means were arsine or square-root transformed and compared by analysis of variance (ANOVA) followed by Waller's separation of means test (SAS Institute 2002). The same procedure was used to compare mean pupal mortalities (the proportions of pupae that failed to yield an adult insect) that occurred under the various regimens.

Results

Effects of a Potential Competitor on Parasitism Rates. 1) *D. areolatus* versus *D. longicaudata* (Fig. 1): Parasitism by *D. longicaudata* was unaffected by either prior or subsequent exposure of hosts to *D. areolatus*. However, parasitism by *D. areolatus* was significantly and similarly lower when host larvae were previously or subsequently exposed to *D. longicaudata*. The ratios of *D. areolatus* and *D. longicaudata* parasitisms obtained when hosts were also exposed to the other species as opposed to parasitisms inflicted by sequential exposures to conspecifics further illustrates the different effects of a heterospecific competitor on *D. areolatus* and *D. longicaudata* (Fig. 2).

2) *U. anastrephae* versus *D. longicaudata* (Fig. 3): Parasitisms by both *U. anastrephae* and *D. longicaudata* were significantly reduced by prior or subsequent

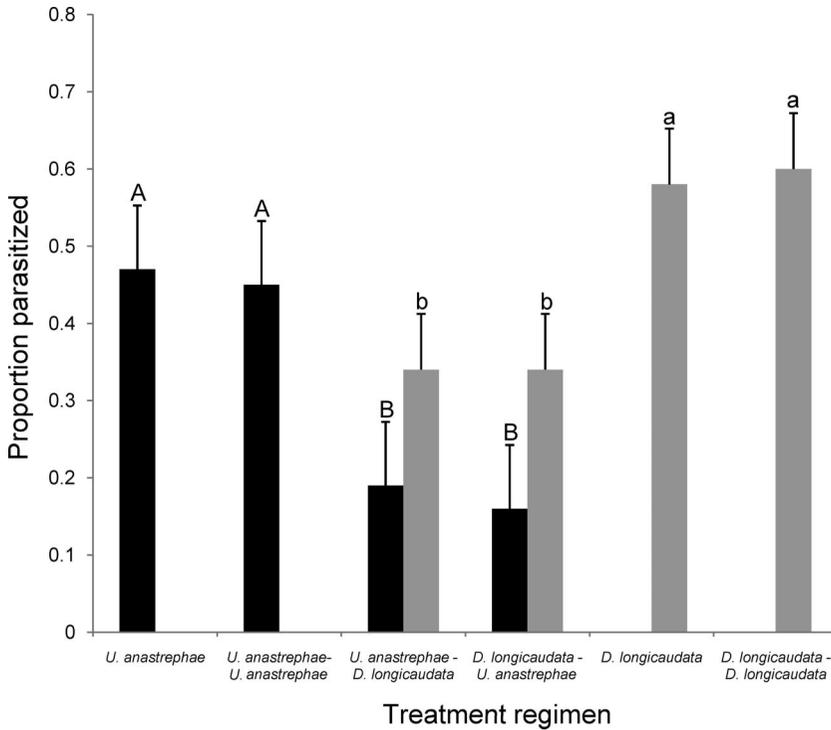


Fig. 2. The parasitism ($n_{\text{parasitoid}_x} / \Sigma$ adult insects) inflicted by a species relative to that obtained in the presence of a heterospecific intrinsic competitor (mean parasitism by parasitoid_x with heterospecific competition or mean conspecific parasitism by parasitoid_x). Mean conspecific parasitisms were taken from *Anastrepha suspensa* host-cohorts that were exposed to two females of the same species sequentially. *Doryctobracon areolatus* (*D. areolatus*), *Diachasmimorpha longicaudata* (*D. longicaudata*), and *Utetes anastrephae* (*U. anastrephae*).

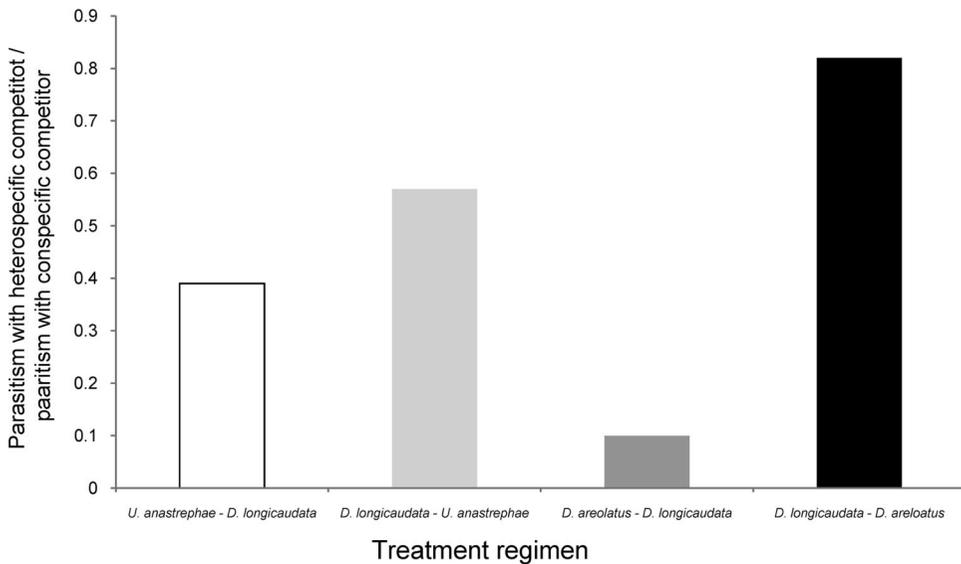


Fig. 3. The mean proportions (SE) of the adult insects that emerged from cohorts of *Anastrepha suspensa* larvae that were the parasitoids *Utetes anastrephae* (*U. anastrephae*) or *Diachasmimorpha longicaudata* (*D. longicaudata*) ($n_{\text{parasitoid}_x} / \Sigma$ adult insects). Host cohorts were exposed to either a single female of a particular species, two females of a species sequentially, or a female of first one species and then another and vice versa. Means sharing a letter were not significantly different (capital letters refer to comparisons of mean *U. anastrephae* parasitisms and lower-case letters to those of *D. longicaudata*).

exposure of hosts to the other species (Fig. 3). There was no evidence that order of host-exposure to the two parasitoids affected parasitism. The ratios of *U. anastrephae* and *D. longicaudata* parasitism obtained when hosts were also exposed to the other species as opposed to parasitism inflicted by sequential exposures to conspecifics further illustrates the similarity of the effect of a heterospecific competitor on *U. anastrephae* and *D. longicaudata* (Fig. 2).

Discussion

In intrinsic competitions, *D. areolatus* larvae were more adversely affected by the presence of *D. longicaudata* than were the larvae of *U. anastrephae*. Moreover, the order in which the competitors were introduced into the host played no significant difference in the outcomes of the competitions. The relatively poor performance of *D. areolatus* in this instance is consistent with its inferior competitiveness when confronted with *U. anastrephae* (Aluja et al. 2013). The greater size of first instar *U. anastrephae* and its larger mandibles may allow it to destroy hatchling *D. areolatus*, and *D. longicaudata* has a similar record of physical superiority over several intrinsic heterospecific competitors (Palacio et al. 1991, Ramadan et al. 1994).

It had been hypothesized that the historic sympatry of *D. areolatus* and *U. anastrephae* depended upon the ability of *D. areolatus* to escape its superior intrinsic competitor by exploiting hosts in larger fruit that were out of the reach of *U. anastrephae* shorter ovipositor (Aluja et al. 2013). If this hypothesis were true, then the introduction of a superior competitor with a longer ovipositor would deny *D. areolatus* its competitor-free-space and it would face extinction. The present demonstration that *D. longicaudata* is such a longer-oviposited superior intrinsic competitor may account for the range contraction of *D. areolatus* in Florida where first it and then *D. longicaudata* were sequentially introduced 40 yr ago to control the recently invasive *A. suspensa* (Eitam et al. 2004).

Both *D. areolatus* and *D. longicaudata* were originally released in extreme southern parts of the state in 1969 and 1972, respectively (Baranowski et al. 1992). While *D. areolatus* initially thrived and inflicted parasitism rates of nearly 50%, it became increasingly rare after the establishment of *D. longicaudata* (Sivinski 1991). At the time of last systematic survey (Eitam et al. 2004), *D. areolatus* occurred only well above Lake Okeechobee in the northern portion of *A. suspensa* range. It was postulated that it had been able to persist in the north through a capacity for relatively longer diapause (Aluja et al. 1998), that is, an ability to better bridge the longer temporal gaps between fruiting of host-trees at higher latitudes. However, several extensive fruit collections throughout its former range in 2009–2011 failed to find any *D. areolatus* and it is either extinct in Florida or its numbers have substantially declined (J.S. et al. unpublished data).

In Mexico, niche separation may be based on both altitude, *D. areolatus* is relatively more common at lower altitudes (Sivinski et al. 2000), and more likely

fruit size or species, *D. longicaudata* is more abundant in large commercial, often exotic, fruits such as *Citrus* spp. than in native fruits (López et al. 1999). Unfortunately, there are only fragmentary accounts of *D. areolatus* pre-*D. longicaudata* distribution and the spatial effect of adding *D. longicaudata* to the *Anastrepha*-parasitoid guild cannot be determined.

What of the distribution of *U. anastrephae* in Florida after the release of *D. longicaudata*? *U. anastrephae* is the only Florida-native of the three parasitoid species and it originally attacked nonpest *Anastrepha* spp. in the extreme southern part of the state (Wharton 1988). With the spread of *A. suspensa*, *U. anastrephae* spread as well and it is now found throughout most of the range of its host (Eitam et al. 2004). While it is not always common, it does not appear to have shared the same local elimination suffered by *D. areolatus*, and this might be because of its relatively better performance in intrinsic competition with *D. longicaudata*. While *D. areolatus* parasitism declined by 90% when *D. longicaudata* was allowed to oviposit either before or after into the same host cohort, parasitism by *U. anastrephae* declined by only 60%. Furthermore, *D. longicaudata* itself suffered when confronted with *U. anastrephae*. Its parasitism fell to 60% of what it had been able to inflict when *D. longicaudata* females had been sequentially given access to the same host cohort. This was in contrast to the negligible effect of *D. areolatus* on the successful development of *D. longicaudata*.

If as suggested, ovipositor lengths have contributed to the present host ranges and distributions of *D. areolatus*, *D. longicaudata*, and *U. anastrephae* then consideration of ovipositor lengths also has implications for biological control tactics. While *U. anastrephae* is native to Hispaniola, *D. areolatus* is not, and the later was recently introduced into the Dominican Republic to control the West Indian fruit fly, *Anastrepha obliqua* (Macquart) (Serra et al. 2011). Because in native sympatry *U. anastrephae* is a superior intrinsic competitor and *D. areolatus* exploits a broader range of host-fruit, it was predicted there would be no negative interactions when the two species were “re-united” and overall parasitism would increase. As of yet, there is no evidence of competitive exclusion of one species by the other. However, the introduction of *D. longicaudata* into Hispaniola has been discussed and this could have more substantial outcomes, as extreme as the eradication of the recently established *D. areolatus* as seen in Florida. It is unclear what effect this might have on overall biological control of *A. obliqua*. Perhaps *D. longicaudata* would inflict greater mortality than *D. areolatus* over the same range of environments, but parasitoid species elimination is a possibility whose consequences should be considered before additional introductions.

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